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FORAGING HABITS, HUNTING AND BREEDING SUCCESS OF LANNER FALCONS (*Falco biarmicus*) IN ISRAEL

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ABSTRACT.—The distribution of Lanner Falcons (*Falco biarmicus*) is restricted to the Mediterranean region and Africa. During 1987–89, data were collected on foraging habits and reproductive success on two breeding pairs of Lanner Falcons at Sede Boqer, in the Negev Desert highlands, Israel. Three hundred and thirty two capture attempts of birds, mammals and insects by the Lanner Falcons were observed, of which 163 (49.1%) were successful. The falcons also pounced on 9 rodents from a perch, or walked on the ground and gathered invertebrates on 27 occasions. A male also hunted bats. Pairs hunted cooperatively during the courtship period prior to egg laying, and also when young accompanied one of the parents on hunting forays. During the fledging period, the male and the female again hunted cooperatively. The overall hatching success for both pairs during the five pair-years was 95.2% and total fledging success was 78.3%.

Hábitos en la alimentación, caceria y reproducción de halcones de la especie *Falco biarmicus,* en Israel

EXTRACTO.—La distribución de halcones de la especie *Falco biarmicus* está restringida a la región mediterránea y Africa. Durante 1987–89 se han recogido datos sobre los hábitos de caza y de reproducción de dos parejas de halcones (*F.b.*), en Sede Boqer, en las alturas del desierto Negev en Israel. Se observaron 332 intentos, hechos por estos halcones, para la captura de aves, de mamíferos y de insectos. De estos intentos 163 (49.1%) tuvieron éxito. Los halcones también embistieron desde una percha sobre 9 roedores; o recolectaron invertebrados, en 27 ocasiones, caminando sobre el suelo. Un halcón macho también cazó murciélagos. La caza cooperativa en las parejas ocurrió durante el período del cortejo, antes de la puesta de los huevos, y también cuando las crías acompañaron a uno de los padres en sus salidas de cacería. Durante el período de los primeros vuelos de las crías, los padres nuevamente cazaron cooperativamente. El total de incubaciones con éxito para ambas parejas durante los 5 años/pareja fue de 92.5%; y el total de éxito en los primeros vuelos fue de 78.3%.

[Traducción de Eudoxio Paredes-Ruiz]

The distribution of Lanner Falcons (*Falco biarmicus*) is restricted to the Mediterranean region (Cade 1982, Salvo 1984) and Africa, especially south of Sahara (Brown et al. 1982) where they inhabit arid regions that receive less than 625 mm of rain per year (Brown 1970). About twenty resident breeding pairs are known from Israel (Yosef 1988). They nest between Eilat in the south to Samaria in the north (Frumkin 1986). During 1987–89, I collected data on foraging habits and reproductive success on two breeding pairs of Lanner Falcons at Sede Boqer, in the Negev Desert highlands, Israel.

STUDY AREA AND METHODS

The study was done in the vicinity of Sede Boqer (30° 52′N 34° 47′E; 475 m above sea level) in the Negev Desert highlands, that are part of the Saharo-Arabian desert belt. This area is arid, with 250–300 biologically dry days per year (UNESCO 1977).

One pair of falcons nested to the west of Divshon Canyon, the second pair nested in the Akev Canyon. I visited nest ledges several times a month, at irregular intervals throughout the year and carried out weekly observations during the breeding season (February–June). During egg laying and incubation, I limited visits to 10 min or less, while I observed through a 20× telescope and/or 10 × 40 binoculars. The nest of the western pair was first discovered in April 1978 by personnel of the Sede Boqer Field Study Center. Although records were kept of the pair's nesting attempts, no data on clutch size, hatching success or fledging success were available prior to my

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Table 1. Food habits of Lanner Falcons at Sede Boqer, Israel.

	PAIR			
	EASTERN	WESTERN	TOTAL ITEMS	PERCENT
Prey taken	72	91	163	100.0
Prey caught in the air			136	82.9
Prey caught from perch			3	1.6
Prey caught by walking			27	15.5
Birds				
Alectoris chukar	29	40	72	43.1
Pterocles sp.	10	11	21	12.6
Columba livia	9	5	15	9.0
Ammoperdix heyi	3	2	5	3.0
Passer sp.	1	3	4	2.4
Streptopelia sp.	—	2	2	1.2
Galerida sp.	1	—	1	0.6
Unidentified	7	4	11	6.6
Total	60	67	127	78.5
Mammals				
Psammomys obesus	2	—	2	1.2
Lepus capensis	1	—	1	0.6
Insectivorous bats	—	5	5	3.0
Unidentified	1	—	1	0.6
Total	4	5	9	5.4
Invertebrates				
Ants	7	6	13	7.7
Grasshoppers	—	5	5	3.0
Beetles	1	4	5	3.0
Unidentified	—	4	4	2.4
Total	8	19	27	16.1

study. The nest of the eastern pair was discovered in 1984 (Frumkin 1986). I collected data on nesting success from the western nest in 1987–89 and eastern nest in 1988–89.

RESULTS AND DISCUSSION

Food Habits and Hunting. All foraging observations were made on the flat loessal plain, Sede Zin, located to the north of the Zin riverbed, in the immediate vicinity of the nest sites (approximate 1 km radius). I observed 332 capture attempts by the Lanner Falcons of birds, mammals and insects. Of these 163 (49.1%) were successful. The western pair made 153 capture attempts and was successful in 91 (59.5%). The eastern pair made 179 attempts of birds, of which 72 (40.2%) were successful. In 82.9% of observations the prey was caught in flight. Most birds (63.2%) were taken from a stoop, often after the falcon had been circling high. At times (5.2% of observations) a falcon dropped below the prey and grasped it from below and behind.

Sixty-nine of the bird prey items captured were chukars (*Alectoris chukar*; Table 1). Other identifiable birds were sandgrouse (*Pterocles* sp.), Rock Doves (*Columba livia*), Sand Partridges (*Ammoperdix heyi*), sparrows (*Passer* sp.), Ring-necked Doves (*Streptopelia* sp.), and larks (Alaudidae sp.).

The falcons also pounced on 9 rodents from a perch, or walked on the ground and gathered invertebrates on 27 occasions. This concurs with the descriptions of Lanner Falcons observed foraging in Africa (Brown et al. 1982). I saw a lanner capturing and carrying a Fat-tailed Sand Rat (*Psammomys obesus*) twice. The female of the eastern pair also was seen in flight with a hare (*Lepus capensis*) in its talons. Because of the proximity of the sighting to

Table 2. Hunting success of adult Lanner Falcons at Sede Boqer, Israel. Data are based on observations during 1987–89. Averages are represented ±1 standard deviation. Data include various kinds of prey (birds, mammals and insects).

	WESTERN PAIR		EASTERN PAIR	
	MALE	FEMALE	MALE	FEMALE
ALONE				
Attempts	43	19	29	49
Kills	19	7	9	26
Percent successful	44.2	36.8	31.0	53.1
COURTSHIP COOPERATIVE HUNTING WITH MATE				
Attempts	11	11	11	11
Kills	5	6	7	7
Percent successful	45.5	54.5	63.6	63.6
BREEDING				
Attempts	34	3	37	4
Kills	14	1	16	2
Percent successful	41.2	33.3	43.2	50.0
COOPERATIVE HUNTING WITH YOUNG				
Attempt	19	13	19	19
Kills	8	8	11	13
Percent successful	42.1	61.5	57.9	68.4
Total attempts	107	46	179	83
Kills	46	22	95	48
Hunting success	43.3 ± 4%	47.1 ± 14%	53.7 ± 7%	58.7 ± 9%

the highway, it is possible that the hare was a scavenged road kill.

The western male also hunted bats. For three consecutive days, during March of 1989, I observed the male foraging at dusk over the community swimming pool. He circled overhead and dived towards bats that were skimming over the water. He chased the bats from behind and above, and caught 5 in 17 attempts (29%). One of the bats captured was a European Free-tailed Bat (*Tadarida teniotis*), the others were Kuhl's Pipistrel (*Pipistrellus kuhlii*). Two of the five bats were taken to the nesting cliff, the others were consumed in a nearby tree. On all occasions the wings were removed prior to ingestion. This concurs with similar observations by Tout (1986), Thomsett (1987) and van Jaarsveld (1988).

During late summer and autumn (mid-June to late November) all observations were of individual falcons hunting separately (N = 47) and feeding alone (N = 22; Table 2). They hunted cooperatively during the courtship period prior to egg laying, and also when young accompanied one of the parents on hunting forays. Adult Lanner Falcons may use cooperative hunting to teach their young different hunting tactics, and to enhance hunting success (Hector 1986). Cooperative hunting has also been reported in Lanner Falcons from elsewhere in the species range (Cramp and Simmons 1980). In late December, males and females hunted cooperatively 11 times. The male mainly flushed and chased the prey (17 of 22 observations), usually in the direction of the female (14 of 22 observations). Upon detecting the female, the prey either turned back toward the male (7 observations) or kept flying into the flight path of the female (12 observations).

From late February to April, when the female was on eggs or with nestlings, the male supplied almost all the food to the female and young (50 to 53 observed visits to nest). The female left the nest area for short periods, during which the male remained in the vicinity. Only rarely was she seen to hunt. On three occasions the female was observed to catch Rock doves. This concurs with descriptions by Brown et al. (1982).

During the fledging period, when young were in

Table 3. Breeding success of two pairs of Lanner Falcons in Israel. The pairs were observed during the years 1987–89.

	WESTERN PAIR			EASTERN PAIR		
	EGGS		YOUNG	EGGS		YOUNG
	LAID	HATCHED	FLEDGED	LAID	HATCHED	FLEDGED
1987	4	4	4	—	—	—
1988	4	3	3	4	4	4
1989	5	5	3	4	4	4
Total	13	12	10	8	8	8
Average	4.3	4.0	3.3	4.0	4.0	4.0
Percent	100.0	92.3	76.9	100.0	100.0	100.0

the vicinity of the nest, the male and the female again hunted cooperatively (32 of 38 observations). The parents then brought prey either to the nest or to the ledge on which the young were perched. After the young had fledged and were capable of flying some distance they accompanied their parents on hunting forays, but only one nestling at a time (70 observations). Young that did not participate remained on ledges in the vicinity of the nesting ledge. Following dispersal of the young, the male and the female remained in their territory, but hunted and fed separately.

Both males were less successful (Table 2) at hunting than their mates (48.9% and 43.3% compared to 58.7% and 47.1% respectively). Except for the western male, the falcons were least successful during the summer when hunting alone. Cooperative hunting between mates enhanced hunting success and was greatest prior to the breeding season. Females had greater success than males (Mann-Whitney U test, $P < 0.05$; Table 2) when cooperatively hunting with young. The overall hunting success of 49.1% is high compared to other *Falco* (e.g., Bird and Aubry 1982, Dekker 1987).

Nest Defense. Most territorial birds defend territories only against their own kind, but some also exclude other species with similar ecology. Some species defend only their nesting sites (Newton 1979). At the nest, Lanner Falcons attacked and drove away larger raptors such as Rough-legged Hawks (*Buteo lagopus*) and Golden Eagles (*Aquila chrysaetos*), but other falcons that nested in the vicinity, kestrels (*Falco tinnunculus*) and Barbary Falcons (*Falco pelegrinoides*), were not attacked. The two pairs of Lanner Falcons seemed to have 'mutually exclusive feeding territories' (Newton 1979).

Breeding Success. Both pairs laid eggs in scrapes on a cliff ledge (see also Brown et al. 1982). Clutches were completed toward the end of February and young hatched in the third or fourth week of March. The young fledged towards the end of April and dispersed from the parents' territory in mid-June.

In the 1987 breeding season, the western female laid 4 eggs, one each at 24 hr intervals. In the 1988 breeding season, the nest was observed when the first young started to hatch. The next day three young had hatched, indicating that young can hatch within 24 hours of each other and that incubation was penultimate or even ante-penultimate (Kridelbaugh 1983). This does not concur with Brown et al. (1982) who state that incubation begins with the first or second egg.

On three occasions I observed young dismember Rock Doves (190–290 g) at the age of 26 d (3 observations). At this age they hopped about the cliff face during the day, often occupying different ledges. Toward sundown, however, they congregated on the nesting ledge. After the young could fly short distances, they kept in vocal contact with each other and usually flew towards the parent with food. At approximately 60 d of age they accompanied their parents on hunting forays.

Reproductive success by the falcons is reported in Table 3. Average clutch size for both pairs was 4.2. Each of the pairs raised only one brood. The overall hatching success for both pairs during the five pair-years was 95.2% and is higher than the 71% found by Brown et al. (1982). Total fledging success was 78.3%. Pairs returned to nest on the same ledges in subsequent years.

Based on my study area, I cannot concur with the conclusions of Brown et al. (1982) and Osborne and

Colebrook-Robjent (1984) that Lanner Falcon nesting density is mainly dependent upon nest site availability. Nesting ledges similar to those used by the pairs studied were widely available and hence this factor was unlikely to limit density. I believe that other limiting factors, are yet to be discovered.

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DO MIGRANT SWAINSON'S HAWKS FAST *En Route* TO ARGENTINA?

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ABSTRACT.—Some observers assert that Swainson's Hawks (*Buteo swainsoni*) do not feed during their migration between North America and Argentina, which lasts 5 or more weeks. Evidence for such a prolonged fast is anecdotal, speculative, and equivocal. A migratory fast of this duration is physiologically and ecologically improbable. It is doubtful that Swainson's Hawks can accomplish fattening of the magnitude necessary for this prolonged fast. Approximately half of the birds have little visible subcutaneous fat when they reach Panama, only about the halfway point of their journey. Although fasting migrants would incur a negative water balance and would need to drink periodically, observations of drinking during migration appear to be lacking. It seems improbable that a highly insectivorous raptor would reject food for a period of 5 weeks or more while traveling through regions which support some of the richest invertebrate faunas in the world; the adaptive value of such a behavior is not apparent.

¿Se abstienen de comer las rapaces migratorias de la especie *Buteo swainsoni* en su ruta a la Argentina?

EXTRACTO.—Algunos observadores sostienen que las aguilillas de la especie *Buteo swainsoni* no comen durante su migración desde Norte América a la Argentina, que puede durar 5 ó más semanas. Evidencias para tan prolongado ayuno son anecdóticas, especulativas y equívocas. Un ayuno migratorio de esta duración es fisiológica y ecológicamente improbable. Es dudoso que estas aves *Buteo swainsoni* puedan lograr un nutrimento de la necesaria magnitud para este prolongado ayuno. Aproximadamente la mitad de las aves tienen muy poca grasa subcutánea visible cuando ellas llegan a Panamá, que está aproximadamente en el punto medio de su travesía. Aun cuando los migrantes incurrieran en un balance negativo de agua y necesitaran beber periódicamente se observa que falta, al parecer, el hecho de beber durante la migración. Parece improbable que raptoras que son altamente insectívoras, omitan comer por un período de 5 ó más semanas, mientras viajan a través de regiones que ofrecen una de las más ricas faunas invertebradas del mundo. El valor que se adapte a tal conducta no es aparente.

[Traducción de Eudoxio Paredes-Ruiz]

The question of whether a particular avian species can meet its energy needs during long distance migration by relying on stored body fat, or by refueling (i.e., feeding) is intriguing. Remarkable examples of premigratory fattening and fasting migration have been documented in a number of avian species, which make long, nonstop flights over oceans, deserts or other inhospitable areas where refueling is difficult or impossible. Other migratory species migrate more slowly, alternating daily periods of movement with periodic rest stops. They typically feed *en route* as they encounter feeding opportunities.

Most migrant raptors use this "stop and go" migration pattern. Slower migrants may maintain somewhat elevated levels of stored body fat during migration, but this moderate fat depot appears to serve mainly as a reserve supply to carry them through periods of food scarcity. They do not store enough premigratory fat to fuel the entire migration. A refueling strategy spares the use of this reserve supply of fat and may augment the fat depot when the migrant finds sufficient food supplies along the way (Berthold 1975).

Several workers have hypothesized that some neotropical raptors (e.g., Turkey Vultures *Cathartes aura,* Swainson's Hawks *Buteo swainsoni* and Broad-winged Hawks *Buteo platypterus*) fast during migration (Smith 1980, 1985, Smith et al. 1986, Houston 1987, 1990). These raptors often fly in large, concentrated flocks (kettles) between their north temperate breeding grounds and their non-breeding areas mainly in Central America or South America. The selective advantage of fasting migration (i.e., total abstention from feeding for prolonged periods) is not intuitively obvious. The stop and go pattern of migration should make refueling possible, unlike non-stop marathons where fasting is obligatory.

This commentary reexamines the evidence for fasting migration in Swainson's Hawks. It critiques the energetic arguments previously used to support the hypothesis, considers the water budget constraints on migration, and examines the ecological plausibility of fasting migration in this species.

The Fasting Migration Hypothesis. Brown and Amadon (1968) reported the "general lore" that these species of raptors do not feed during migration. Smith (1980) presented the following evidence to support the fasting hypothesis: 1) the scarcity of published accounts of migrants seen feeding, 2) the reports from country people in Panama of both Swainson's and Broad-winged Hawks in weak condition on the ground below roosts and similar reports of exhausted Swainson's Hawks in Argentina, and 3) the absence of feces and pellets below roosts where thousands of the hawks had roosted the previous evening. Smith (1980) states that "most of the evidence is circumstantial, but, in total, supports the fasting hypothesis." Smith has argued that the massed flights and huge communal roosts would likely preclude most individuals from obtaining significant amounts of food under such crowded conditions, and that it would be more costly to forage and feed than to fast.

Smith (1985) elaborated on the scenario of an "anorexic migration strategy" by speculating that Swainson's Hawks feed copiously while wandering south in small groups, then cease feeding at about 30°N latitude when they begin massed flights. Smith (1985) estimated that the fasting migration lasted 50-60 d, based on the dates of passage of the first observed massed flocks at Las Cruces, New Mexico and Panama City and the time of arrival of Swainson's Hawks in Argentina. The duration of fasting migration was later revised downward to 37.5 d by assuming that a hawk averages 240 km/day throughout the 9000 km journey (Smith et al. 1986). A key assumption in their fasting migration hypothesis is that thermal soaring is a highly efficient mode of travel with very low energetic costs, only twice the basal metabolic rate.

Weaknesses in the Fasting Migration Hypothesis. The circumstantial evidence for prolonged fasting can be refuted in several ways. Concentrations of hundreds of migrating Swainson's Hawks have been observed as far north as Saskatchewan (Houston 1987, 1990), Washington and Montana (Bent 1937). These locations are 1500-2000 km north of the presumed extent of massed migration and would apparently add at least another week of travel to the required duration of fasting, assuming the rationale that massed flights preclude feeding. Smith (1985) acknowledged some published accounts of Swainson's Hawks feeding in large groups in Texas (Littlefield 1973) and in Costa Rica (Slud 1964). Large assemblages of Swainson's Hawks also have been seen feeding in Washington and California (Bent 1937), Idaho (Johnson et al. 1987), and near Veracruz, Mexico (M. Ramos, pers. comm.).

Although mass roosts of these migrant hawks in Panama are reported to lack feces, feces were present at mass roosting sites of migrant hawks in Arizona (Henshaw 1875 in Bent 1937) and in Mexico (M. Ramos, pers. comm.). It is possible that during the first hours of light each day, before thermal soaring is feasible, most hawks disperse from roosts, regurgitate pellets and then feed mainly on insects. Most of the resulting excrement from that early morning meal would be eliminated during the following 10-hour flight period. Rates of food passage through the gastrointestinal tracts of raptors have not been determined, but judging from the rates of food passage in other avian species, it is reasonable to assume that a Swainson's Hawk would eliminate the bulk of an early morning meal before arriving at the evening roost (G. Duke, pers. comm.). If hawks have virtually emptied their gastrointestinal tracts before they enter an evening roost, little fecal or pellet material should be found beneath an infrequently used roost.

Reports of southbound hawks arriving in a weakened condition in Panamanian roosts (Smith 1980) suggest that some hawks become undernourished when they reach maximally crowded conditions in the geographical bottleneck of the Central American isthmus. However, undernutrition could be due to poor foraging success, rather than absolute fasting. The presence of emaciated migrant Swainson's Hawks in Central America indicates that some hawks deplete their limited energy stores much earlier than should be the case according to the fasting migration hypothesis. Indeed, the observation of emaciated Swainson's Hawks in Panama supports the alternative hypothesis that migrant hawks typically carry only moderate fat reserves which may be seriously depleted if the birds fail to find sufficient nourishment along the way.

Problems with the Predicted Duration of Fasting. The speculation that hawks fast for 5-8 wk during migration is a major weakness of the fasting hypothesis. Could a hawk, even at rest, survive such a long period of food deprivation? Using Smith's

(1980) original estimates of migration duration (60 d) and Swainson's Hawk lean body mass (900–1000 g), approximately 420–450 g of stored fat would be required for standard metabolism (SMR) alone (Aschoff and Pohl 1970). This fat depot would constitute 45–47% of the original body mass. In this computation, the fat has not been included as metabolically active tissue.

The required amount of fat storage would have to be even larger than the above estimate, because a bird in migratory flight should require more energy than a bird at rest (e.g., 2 × SMR; Baudinette and Schmidt-Nielsen 1974), and a soaring bird carrying such a heavy burden of body fat should expend more energy per distance traveled than a bird at its optimal flight mass.

Smith's (1980) original estimate of Swainson's Hawk body masses (900–1000 g) is similar to the body masses determined by Craighead and Craighead (1956) (♂ = 908 g; ♀ = 1069 g), Fitzner (1978) (♂ = 747 g; ♀ = 1080 g), and Smith et al. (1986) (♂ = 723 g; ♀ = 966 g). These data indicate that females average about 160–260 g heavier than males. In later publications Smith (1985) and Smith et al. (1986) arbitrarily select a lean body mass of 600 g for male Swainson's Hawks, a seemingly low estimate, to compute the energy cost of migration. They did not attempt to model the energetics of females which reportedly weigh 900–1000 g.

Smith (1985) stated that if the lean body mass of a Swainson's Hawk is 600 g and its fat mass is 240 g "it could easily make the flight between Argentina and southern North America in 60 days without feeding." Smith's estimate, which assumes the catabolism of 4 g of fat per d (or 159 kJ/d; assuming that fat averages 39.7 kJ/g), would only supply 77% of the energy required for standard metabolism of a non-passerine bird of that body mass (Aschoff and Pohl 1970), or 88% of the estimated resting metabolism of a diurnal raptor of that size (Wasser 1986). Smith's (1985) metabolic estimate is far below that which would reasonably be expected for a bird in active migration.

Using a computer modeling technique, Smith et al. (1986) offered a revised estimate indicating that a male Swainson's Hawk (lean body mass = 600 g) would catabolize approximately 8.8 g of fat per day or 330 g of fat for a 9000 km flight. In the model, they assumed that the energy cost of flight is only twice the basal metabolic rate, roosting metabolism is 80% of standard metabolism, and migration speed averages 240 km/d (a 37.5 d journey). Furthermore, they contended that the storage of such a large fat depot (55% of the lean mass) is "physiologically reasonable" (Smith et al. 1986).

Problems with the Necessary Amount of Stored Fat. The implausibility of a large raptor storing enough fat to sustain a fasting migratory journey lasting many weeks is another major weakness of the fasting migration hypothesis. It is doubtful whether Swainson's Hawks can accomplish fattening of the magnitude necessary for this prolonged fast. An exhaustive study of the body composition of 688 migrant Goshawks (*Accipiter gentilis*) in Sweden showed maximum fat levels of 14.1% and 17.2% of body mass in males and females, respectively (Marcstrom and Kenward 1980). Gessaman (1979) reported premigratory fat levels in American Kestrels (*Falco sparverius*) averaging 5–7% of the total body mass.

Little is known about the size of fat deposits of most diurnal raptors, but workers have frequently assumed that substantial differences in the average body masses of adults at different times of the year represent changes mainly in the amount of stored fat. The greatest body mass fluctuations in adult raptors have been recorded as the measured differences in body mass of females in egg laying condition versus non-breeding condition. Newton (1979) described the "great increase" in the mass of female European Sparrowhawks (*Accipiter nisus*) from a prelaying average of 300 g to an average at the peak of laying of 345 g, an increase of 15%. Similarly, female American Kestrels average approximately 29% heavier during the laying period in May than during July, the month of their lowest average mass of 109 g (J.S. Kirkley, unpubl. data). Extreme levels of premigratory fattening (30–47%) have been found only among small birds which make long, nonstop flights; the average fat reserves of even the larger limicoline birds (i.e., sandpipers and plovers) do not exceed more than 20% of the live mass (Berthold 1975).

The limited information on raptor body mass fluctuations does not support the contention that male Swainson's Hawks can store fat equal to 55% of their lean mass or 35% of their total body mass. Female Swainson's Hawks would require proportionately similar increases in their body masses, because their 160–260 g larger body masses should, according to allometric predictions, require the catabolism of at least 17–23% more fat than is needed for males. Smith et al. (1986) assumed that the additional energetic costs of carrying these large burdens of body fat would be taken into account by using total body mass rather than lean mass in the allometric equations for estimating energy expenditures. Whether this allowance actually overestimates the true rate of energy expenditure, as Smith et al. (1986) contend, remains an unanswered question.

Quantitative measurements of stored fat in Swainson's Hawks are lacking. Smith et al. (1986) estimated the relative fatness of southbound hawks captured from mass roosts in Panama by inspecting their visible subcutaneous fat. The investigators judged only 8% (5 of 64) of the Swainson's Hawks to be very fat (fat index = 3), whereas 41% of the juveniles and 51% of the adults had little or no visible fat (fat index = 1 or 0). Low subcutaneous fat indices in a migrant should indicate that body fat is nearly depleted, because subcutaneous fat is considered to be the last region of body fat to be utilized (Blem 1989).

These fat index data pose a serious objection to the fasting migration scenario. Nearly half of the hawks examined had practically exhausted their fuel supply at slightly less than the halfway point of their hypothetical 9000 km fasting journey. Swainson's Hawks, at that point, should be carrying more than half of the original fat depot (at least 165 g of fat in males, or 28% of their lean body mass). A hawk (600 g lean mass) possessing over 165 g of fat should certainly have sufficient subcutaneous fat to be visually judged "very fat." In contrast, only 8% of the Swainson's Hawks were judged to be "very fat." These data alone refute the idea that most Swainson's Hawks fast for the entire duration of migration.

Water Budget Considerations. The respiratory water losses of fasting migratory birds should exceed their rates of metabolic water production; this negative water balance will be even more severe if substantial cutaneous water losses occur (Hart and Berger 1972). An estimated rate of fat oxidation of 8.8 g/d (Smith et al. 1986) would yield 9.4 g of water, assuming oxidation of one gram of fat yields 1.071 g of water (Schmidt-Nielsen 1964:30). The estimated minimum rate of evaporative water loss of a resting 600 g hawk would be approximately 18.3 g/d (Crawford and Lasiewski 1968, equation 6). The calculated minimum water deficit would, therefore, be approximately 9 g/d (1.5% of lean body mass). This value probably underestimates the daily water deficit of a fasting hawk, because rates of evaporative water loss should increase with the higher rates of pulmonary ventilation expected to accompany elevated metabolism during flight. Higher rates of cutaneous evaporation should also result from increased convection during flight. The magnitude of the water budget deficit would increase even further if there were any excretory water losses or if fasting hawks ever had to pant to cool themselves in the high temperatures and intense sunlight of those subtropical and equatorial regions.

Basal rates of evaporative water loss would, alone, amount to more than 10% of a fasting hawk's lean body mass per week. With the likely routes of additional water loss, a fasting migrant hawk probably would need to drink, each week, a quantity of water equal to 15–20% of its lean body mass to offset its water deficit. Normally, raptors do not drink water, because they obtain sufficient water from the prey they consume (Bartholomew and Cade 1963). If the fasting migration hypothesis were valid, massed flocks of fasting hawks should be seen occasionally drinking at open water (undoubtedly a memorable spectacle), yet I have not read or heard of such behavior. Lack of evidence of drinking lends support to the contention that migrating hawks must be maintaining their water balance by feeding *en route*.

Ecological Considerations. A final argument against the fasting migration hypothesis is the one that seems most obvious from an ecological standpoint. Prolonged fasting migration is only typical of birds which fly nonstop over inhospitable barriers such as deserts or bodies of water. What is the ecological barrier posed by the migration route of Swainson's Hawks? Apparently none. Like many species of gulls, Swainson's Hawks are known to congregate on the ground in large flocks and to gorge themselves on grasshoppers, crickets and other insects (Bent 1937, Johnson et al. 1987). Are the flocks of Swainson's Hawks always so large as to preclude them from exploiting insects they encounter throughout the 9000 km journey? It is difficult to imagine that Swainson's Hawks would terminate all feeding during those many weeks of travel through the tropics and subtropics, particularly since those areas are rich in insect abundance. In conclusion, there appears to be no obvious ecological necessity for prolonged fasting by any of the raptors migrating through the Neotropics.

Insects should be especially abundant during the southward passage of hawks in October, because this is the tropical rainy season with its accompanying resurgence of vegetation and insect life. Rainstorms lasting several days are not uncommon in the subtropics of Mexico and Central America, and these storms are known to effectively ground Swainson's and Broad-winged Hawks (M. Ramos, pers. comm.). When thermal soaring migration of these hawks is delayed, as it is on rainy days and during the first hours of light each morning, the hawks should be expected to disperse from their roosts and hunt for food.

Speculations which attempt to extrapolate the behavior of southbound Swainson's Hawks in Panama to their entire 9000 km journey may lead to erroneous conclusions. Questionable energetic parameters may add overly optimistic support for the plausibility of fasting migration. Further studies are needed which actually document the behavior of members of individual flocks for several consecutive weeks. These studies should include continuous monitoring of massed flocks as they move through Mexico, Central America and South America. Predicted behavior, based on the considerations presented in this commentary, would include opportunistic feeding by hawks when they are not involved in thermal soaring, and no drinking. Periods of fasting or undernourishment, should be short-term, and feeding should commence when insect infestations and other prey are opportunistically encountered.

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